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HEREDITY AND SEX.*

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All higher organisms, whether plant or animal, have sexuality. It is only the very lowest that lack the sex potentiality and are truly nonsexual. The blue-green algæ, for example, appear to be such organisms. Apparently their protoplasm is not organized in such a way that sexual states can arise in it. But with an advance in cell organization, probably involving a more advanced and more complicated nucleus with definite chromosomes, the sex potentiality is introduced and the protoplast may then pass into any of the three conditions commonly manifested by sexual organisms, namely the female state, the male state, or the neutral state.

When sexuality first appeared it was manifested only as a physiological state. No dimorphism is in evidence. The sexualized cells simply take on a peculiar property, for the time being, by which they are attracted in pairs, come together, and fuse into one unitary protoplast. This is a most remarkable process. Although the chromatin from the two gametes is inclosed in the same nuclear membrane, it is not commingled but the individual chromosomes from each parent gamete retain their identity and hence a diploid condition is established in respect to the chromosomes. After the fusion, all evidence of a primary female state (p. +) or of a primary male state (p. —) disappears in a neutral condition of the cell. But when the zygote undergoes its first division after the fusion process, or at some subsequent division, a second primary sexual phase is inaugurated, but this time it does not involve the protoplast as a whole but only the individual chromosomes in the diploid nucleus. These bodies now show the same remarkable attractive

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property toward each other in specific pairs as the gametes did formerly, undergoing a primary plus (+) and minus (—) sexualization, and thus come together as fused but not commingled pairs and are then separated to the opposite poles by the division spindle. These two processes of primary sexualization—the conjugation of gametes resulting in a unitary protoplast with a diploid condition of the nucleus and the reduction division resulting in a specific synapsis of chromosome mates and their segregation—are present in all organisms with normal sex potentiality. The diploid chromosomes are sexually neutral in respect to each other, that is they do not have the primary sexual plus and minus states, except during the reduction division phase no difference whether the tissues in which they are situated are in the secondary female state, in the secondary male state, or in the neutral state. As the result of the evolution of the primary sex potentiality, the lowest sexual organisms, therefore, exist in one of the three conditions, primary female state, primary male state, and neutral vegetative state and the chromosomes as individuals may partake of these states along with the state of the cell as a whole or as individuals independently of other parts of the protoplast. The neutral state of the cell may occur both between fertilization and reduction and between reduction and fertilization. The neutral state may disappear in fertilization or it may continue for many vegetative divisions. Likewise reduction may be followed by an immediate primary sexualization of the entire protoplast, or there may be many vegetative divisions following with a completely neutral condition of the haploid cells. Thus the primary sex potentiality is a property of sexual organisms, manifesting itself in various peculiar states during the cell lineage cycle. The potentiality is not inherited as a male potentiality, a female potentiality, or a neutral potentiality since the same complement of chromosomes with the same heredity may exhibit all three states from time to time.

In the progressive evolution of plants and animals the time of sex determination is shifted backward from the mature condition of the gametes to the beginning of gamete development, and thus a dimorphism arises in an orthogenetic progression until the extreme is reached in the highly dimorphic egg and sperm. This dimorphism of egg and sperm as contrasted with the more primitive isogamous condition is characteristic of all higher plants and animals. The heredity

determining the gradients is never lost. The dimorphic character expression which appears in the sperm and egg may not be caused by the primary male and female states themselves, but perhaps by secondary states which may precede them. Since we have no means at the present time of determining the actual differences between primary and secondary states except through the activity of the cells sexualized and no means of ascertaining whether the primary states of the gametes are preceded by secondary states, it is of no special importance to distinguish between them at this point in the ontogeny.

In some, more advanced organisms partial primary sexual states may arise giving the cells the property of attraction but not of fusion, or of cytoplasmic fusion for the time being. At a later stage primary sexualization is completed and fusion of the nuclei then takes place promptly. The further progress in the evolution of sex is the appearance of secondary sexual states and secondary sexual dimorphisms. These potentialities are universally present in all the higher plants and animals. This evolutionary progress is brought about by the introduction into the hereditary mechanism of the protoplast of multicellular organisms of a potentiality, or set of potentialities, by which the sexual state is determined in the ontogeny before the time of gametogenesis has been attained. The cell lineage passes from a neutral vegetative state to a sexual vegetative state, either male or female, and in consequence of these states the hereditary expression of characters is modified, giving rise to secondary sexual dimorphisms, the so-called secondary male and female characters. Since a large part of the lower multicellular organisms, which have heterogany, are hermaphroditic and also the greater part of the heterosporous sporophytes bisporangiate individuals, it follows that in the greater number of plant species, as well as in hermaphroditic animals, there is really a trimorphism normally present, consisting of the neutral tissues and organs, tissues and organs with secondary female characters, and tissues and organs with secondary male characters. All these states are but phases in the development of the individual organism and are developed from protoplasts having a common heredity and with exactly the same complement of chromosomes. Neither the specific character of the heredity involved nor the shifting of chromosomes with the hereditary potentialities can have anything to do with the matter, for the simple reason that no shifting is taking place.

The secondary sexual states have been defined as having the property of influencing the functional activity of the cell in such a way that the hereditary expression is changed. The same hereditary complex gives a different character when the secondary male state is present than when the secondary female state is present and thus a sexual dimorphism results either through an influence on latency and activity of the various hereditary factors present or else by causing the factors to act in a different way under the two conditions. The phenomena of sexual expression are the same in diecious plants. In many genera containing both monecious and diecious species there is absolutely no apparent difference in the dimorphic characters except that in the first only a part of the system is involved in the one sex expression or the other while in the second the entire individual is involved.

The secondary sexual state, as manifested in the protoplast as a whole, always precedes the primary state and in the higher plants with an alternation of generations the sexual states are normally determined but once in the life cycle. When the secondary male state or the secondary female state is once established it remains underchanged, except in case of abnormal sex reversal, even through the reduction division, until the primary sexual state is attained in the gametes and neutralization is accomplished in fertilization. This is true for all heterosporous plants except the comparatively few diecious species and the statement is true for the diecious species also except that in this case fertilization may not end in neutralization. It must be emphasized that it is not proper to consider any cell of a sexual organism as having only male potentiality, neutral potentiality, or female potentiality. But the proper mode of thought, agreeing with the actual phenomena known and to be attained through experiment, is that any given cell has the sex potentiality which for the time being is in the male condition in respect to its functional activity and morphology, in the neutral condition, or in the female condition. Any of these states are potentially possible whether the given cell lineage is diploid or haploid and in any given sexual state for the time being. Such series can be observed or produced in any number of diecious, monecious and bisporangiate-flowered species as well as in haploid and diploid moss protonemas.

The whole modern development of the science of sex as postulated on Mendelian notions shows up in an absurd light

when one considers carefully the enumeration of facts given above and a multitude of others that might be adduced. How has it come that sex was considered Mendelian when we have known from the beginning that in the higher plants, for example, the sexual states and sexual dimorphisms are never changed, are never determined, and are never segregated at the time when the chromosomes with their hereditary potentialities are segregated? There is no real analogy between sex expression in the individual and the alternative inheritance of dominants and recessives in Mendelian heredity. Any race may contain only one of these Mendelian allelomorphs, for they are merely units of subordinate importance, but a race, whether with hermaphroditic or unisexual individuals, must have potentialities for both sexes if fertilization and reduction are to occur at all. Dominants and recessives are not phases of the same potentiality but are distinct, segregative potentialities whereas femaleness and maleness and neutrality are phases of a general sex potentiality in the same individual and only in advanced forms does a single condition usually appear in the individual and here the condition may also be reversed without change of the heredity present as has been repeatedly done in many species by direct experiment. Furthermore, the presence of a secondary male or female state in the protoplast does not interfere with the development of primary plus (+) and minus (—) reactions between the synaptic chromosome mates. When the sex of either a unisexual individual or a unisexual branch of a hermaphroditic individual is reversed, the entire complex of characters of the one sex or the other is normally expressed as a whole, because the given complement of sex characters is but the result of the peculiar bent given to the hereditary expression through the influence of the state present. The only exception to this arises when special heredities are present or lacking in the allosomes which would, of course, cause special expressions of the allosome-linked factors.

Any given hereditary constitution will give a special functional gradient, in the normal environment, which will determine the point in the ontogenetic cycle when the sexual state will be determined one way or the other. These different types of heredities form, like all fundamental evolutionary movements, a definite orthogenetic series. In every case the physiological state through which the sex is determined from the neutral condition to the plus (+) or minus (—) condition,

or is shifted from one sexual state to the other at a given point, is due to a hereditary constitution inherent in the cell. One or more potentialities in combination with the environment determine what the physiological state is at this point. Changing either the hereditary potentiality or the environment sufficiently to change the functional state will shift the point of determination at which the sex balance will be tipped one way or the other.

If we should attempt, at the present time, to extend the theory of Mendelian potentialities to the organism as a whole, to the property of protoplasm by which it is able to carry on respiration or assimilation, to the potentiality or property that determines whether the sex shall be determined in the gametophyte or in the sporophyte, to the properties that distinguish the great phyla, to the profound dimorphism exhibited between gametophyte and sporophyte in the life cycle, to the dimorphic expression of sterile and fertile shoots, to the dimorphism of foliage leaves and sporophylls on the same individual, to the dimorphism of root and shoot, the attempt could not but be regarded as fantastic. Yet the Mendelian conception of sexuality when considered from the standpoint of the actuality of sex phenomena is just as impossible. The notion that many have that an individual with sex potentiality cannot be wholly neutral but must be either male or female is equally fantastic. The sporophyte of a fern shows no maleness nor femaleness. The moss sporophyte shows no sexual dimorphism. Yet we know that the sex potentiality is there, and without changing the chromosome complement in the cells, without subtracting or adding a single gene, we can take this homosporous sporophyte and compel its sex potentiality to produce both normal secondary male and female characters and also primary male and female states. It is entirely wrong to say, like Goldschmidt and others, that sexuality is represented by M (male sex genes) and F. (Female sex genes). If we were rash enough to postulate genes for the various sex conditions we would certainly demand an N. (neutral genes) for fear that homosporous sporophytes would otherwise disappear from the earth. And while we were in the gene-making business we would want a gene for the primary female state which appears in the egg and another one for the primary male state which appears in the sperm. Goldschmidt and others of like mind are simply confused by the phenomenon of sex reversal which they are

not able to fathom, apparently because they hold to a static notion of the organism rather than conceiving of it in terms of growth gradients, even though they may profess to hold to the physiological conception of heredity. Every cell of a sexual organism has the potentiality of passing, in its lineage, into the male and female and neutral states and expressing structures corresponding to these three conditions as will be shown below.

Sexuality then is due to a potentiality of a general nature and when this potentiality is present a cell may pass into any of seven peculiar states and develop characteristic activities peculiar to each state. The seven general states are to be considered as a gradation system and each of the states can be present in different degrees of completeness and intensity. The seven states are: 1. Complete primary female state, 2. Incomplete primary female state, 3. Secondary female state, 4. Neutral state, 5. Secondary male state, 6. Incomplete primary male state, 7. Complete primary male state. The incomplete primary female and male states are in evidence only in certain thallophytes so need not be considered generally. But the five states are usually to be met within most of the sexual plants. The neutral state must not be confused with a vegetative state since there is neutral vegetative growth and activity, as in homosporous sporophytes, female vegetative growth and activity, as in female gametophytes and carpellate sporophytes, and male vegetative growth and activity, as in male gametophytes and staminate sporophytes. Now the time and mode of appearance of sexual states in the ontogenetic cycle is conditioned on a multitude of different hereditary constitutions. Each type is conditioned by a distinctive type of heredity controlling the functional gradient in relation with the environment in which the organism normally lives. A change of environment will, if extreme enough, change the normal mode of appearance and condition of the sexual states naturally developed, especially in the higher, more extreme forms as in monecious and diecious species and in the autoicous and unisexual gametophytes of homosporous Metathallophyta.

The following list gives the typical cases presented by the plant series.

1. The lowest organisms, which have a hereditary constitution without sex potentiality. Examples—*Merismopedia*, *Nostoc*.

2. Organisms which have a hereditary constitution which produces functional gradients that permit of primary sexual

states only and these arising only in the gametes after their complete development. The gametes are, therefore, completely isogamous and the other cells in the lineage are always completely neutral. Examples, *Diatoms, Desmids, Sphaerella, Ulothrix.*

3. Some lower organisms have a hereditary constitution that causes sexual states to arise in the gametes before comp'ete maturity. Thus the completion of the development is carried on under the influence of one or the other sexual states and a partial or moderate sexual dimorphism of the gametes is produced. Examples—*Pandorina, Bryopsis,* some species of *Spirogyra.*

4. Organisms that have a herditary potentiality which causes sex-determination to take place at the very beginning of gametogensis, and thus producing extremely dimorphic gametes, the usual condition of heterogamy. Examples—*Volvox, Sphaeroplea.*

5. The herdity of the organism is such that a functional gradient is developed which produces a condition that the sex-balance is tipped at the beginning of the development of the gametangia, resulting in decidedly dimorphic gametangia as well as decidedly dimorphic gametes. There is a secondary sexual state and a secondary sexual dimorphism established before the primary dimorphism appears in the gametes. Examples—*Monoblepharis, Vaucheria sessilis, Coleochaete.*

6. The herditary potentiality produces a gradient that develops the condition for sex determination in the vegetative phase sometime before the gametangia proper appear, giving rise to secondary sexual dimorphism in the vegetative parts of the gametangia and beyond, as wel as secondary dimorphisms in the gametangia and primary dimorphisms and primary sexual states in the gametes. Examples—*Chara, Fucus evanescens, Vaucheria synandra, Oedocladium protonema.*

7. Organisms, either haploid or diploid, in which the hereditary constitution is such that a physiological condition arises at the very beginning of the ontogeny, or in the spore from which the individual originates, which indues a sex determination and thus the entire individual is unisexual, either a male or a female. This is the normal unisexual condition present in some organisms with a simple haploid sexual cycle and in some with a simple diploid sexual cycle. Examples—*Rhizopus nigricans, Fucus vesiculosus.*

8. Organisms with a typical antithetic alternation of generations in which the hereditary potentialities are such that the gametophyte is sexually neutral up to the time when the gametangia develop and the ontogenetic gradient arrives at the point of sex determination just at the beginning of the formation of the gametangia. There is thus secondary sexual dimorphism of the gametangia and primary sexual dimorphism of the gametes but the sexual states being neutralized in the fertilization process, the sporophyte remains entirely neutral, its sex potentialities being completely latent under the functional gradients established. Thus there is a complete lack of sexual dimorphism and sexual states in the normal sporophyte and the same condition holds over in the vegetative phase of the gametophyte up to the time of the appearance of the incepts of the gametangia. The gametophyte is synoicous. Examples—*Fosombronia foveolata, Bryum arcticum.*

9. The organism is in general the same as in the 8th type but the hereditary constitution is such that the reproductive branch of the gametophyte passes first into the one sexual state, either male or female and after a time the gradient of the growing branch changes and a sex-reversal takes place, the later development of the growing bud giving rise to the opposite kind of gametangia from what were developed first. This is the paroicous condition. Examples—*Cephaloziella elegans, Catharinaea undulata.*

10. Organisms with an antithetic alternation of generations in which the heredity is such that incipient reproductive branches are determined in the secondary male and female states which remain without reversal in the given branch. The gradients which arise in the branches are so evenly balanced that part of them fall into the secondary male state and part into the secondary female state. The conditions of the ontogenetic gradients are, therefore, quite different from those in the 9th type but are similar to the balance produced in certain spores and zygotes in which the poise of physiological state is also so delicate that about half fall to the male condition and about half to the female. These are the organisms with autoicous gametophytes. Examples—*Cephaloziella hampeana, Hypnum riparium.*

11. Certain mosses with branched protonema whose hereditary potentialities are of such a nature that sex determination apparently takes place in the incipient gametophore buds,

each entire scaly gametophore arising from the protonema being either completely male or completely female. No cases definitely established. In some species the female plant apparently gives rise to secondary protonemata from which males develop. Example—*Camptothecium lutescens.*

12. Bryophytes and homosporous pteridophytes in which the sex is determined in the tetraspore. In a few species allosomes are present and are segregated in the reduction division. These allosomes appear to have a definite sex association and may have differential heredities which produce differential functional gradients so that under the usual conditions the sex balance always falls in a given direction in the given case. In the sporophyte these allosomes have no influence, the sporophyte being completely neutral. Regeneration in the sporophyte tissue would probably cause sexual states to appear as has been discovered for numerous mosses. In the vast majority of cases no allosomes have been discovered in plants of this type, as in many unisexual liverworts, mosses, and homosporous pteridophytes like *Pteretis nodulosa* and *Equisetum arvense.*

In the two last mentioned species, sex reversal in both directions is easily induced experimentally. Now these individuals are haploid and there is therefore no correspondence with the notion that their unisexuality is produced by the segregation of sex-determining chromosomes or factors. There is no more basis for such an assumption than for that which considered that gametophytic and sporophytic dimorphism was dependent on haploid and diploid conditions. The remarkable dimorphism exhibited between gametophyte and sporophyte can be produced in the diploid condition without any change of chromosomes or hereditary potentiality. This shows the superficiality of the view that to obtain unisexuality we must in some way be segregating male-producing or determining herdity from female, or male-producing chromosomes from female-producing chromosomes. It is remarkable that in spite of an endless array of experimental evidence, purely fantastic ideas still sway a considerable portion of biologists who cannot get beyond a crude biological confession of faith which was formulated not through a consideration of the actual phenomena of sexuality in relation to heredity and the life cycle but almost wholly through a blind belief in a series of false biological postulates. In changing from one sexual state to the other it

is often much easier to make the change in one sex than in the other. Thus in the ostrich fern it is much more difficult to change male to female than female to male, presumably not because of a lack of potentiality but because of the greater special differentiation of the male gametophyte in this case. Examples as indicated above—*Marchantia polymorpha, Sphaerocarpos* sp., *Mnium punctatum, Equisetum arvense, Pteretis nodulosa.*

The condition in some mosses of unisexual haploid gametophytes and completely neutral diploid sporophytes presents certain aspects fundamentally important to a correct understanding of sexual phenomena in general. The neutrality of the sporophyte is not produced by the balancing of chromosomes or genes of opposite potentialites but because of a condition and gradient established at the time of fertilization which begins a certain differentiation cycle from which the individual normally does not depart throughout its entire ontogeny, ending in determination and death. Now, as intimated above, we know from various experiments, made by various investigators on unisexual mosses, that a protonema can be sprouted from the neutral diploid sporophyte tissue and a new gradient established producing the marvelous result that the same complement of chromosomes with the same hereditary potentialities which produced a neutral or so-called "non-sexual" sporophyte now develops a sexual gametophyte, and furthermore, sometimes this gametophyte is hermaphroditic but occasionally it is again unisexual showing pure male or pure female expression.

One of the more recent investigations along this line was carried out by Schweizer on *Splachnum sphaericum.* The diploid protonema regenerated from the diploid tissue of the sporophyte, although it usually produced hermaphroditic gametophytes nevertheless also produced some pure male and some pure female gametophores, which is the normal condition of the haploid gametophyte. It is perfectly plain, therefore, that the sex-determination and sex-differentiation are dependent on functional states—differentiation states and constancy of differentiation after determination—and not at all on differential heredities, since, with the same heredity present, the functional gradients in the several cases nevertheless bring out pure female, pure male, and hermaphroditic gametophores.

After passing the twelve more striking types in which the sex is normally expressed in the gametophyte, we come to the heterosporous, higher plants where a remarkable shift takes place, an hereditary constitution now having evolved that sooner or later springs the sex balance in the sporophyte; in other words causes some cells to pass into the secondary male state, some into the secondary female state, and in the majority of cases some into the neutral state; whereas all the previous sporophytes with their diploid chromosome complements have normally always developed in a completely neutral condition. Furthermore, the evolutionary movement continues in exactly the same way as it did in the gametophyte. The first phase shows a sex-determination taking place only at the beginning of sporangium development and this is followed by evolutionary movements in a multitude of cases in which the final forms always have their sex determined at the very beginning of the sporophyte ontogeny.

13. The plant has a hereditary constitution which produces a functional gradient in the diploid sporophyte of such a nature that a neutral vegetative body is developed but when the point in the determinate process of the sporophyll is reached where sporang a are developed in the sorus, the incepts of the sporangia pass into the secondary sexual states, some to the secondary male state, and some to the secondary female state, thus giving rise to secondary sexual dimorphisms in the sporangia themselves and their stalks. This secondary sexual state also changes the activity of cell division greatly so that many divisions usually occur in the sporgenuous tissues of the microsporangium and comparatively few in the sporogenous tissue of the megasporangium.

The megasporocytes are also all destroyed in the megasporangium except one. These differences show the profound influence which the secondary sexual state may exert on the activities of the cell. Since sexuality has nothing to do directly with heredity, there is no influence on the sexual states during or after the reduction division. The microsporocytes which are in the secondary male state permit of the primary plus (+) and minus (—) sexualization of their diploid sets of chromosomes with consequent synapsis and segregation. All four cells remain in the secondary male state and produce a tetrad of microspores. Exactly the same process takes place in the megasporocyte which is in the secondary female state. All

four of the resulting cells remain in the secondary female state and develop as four megaspores. In many cases, however, only one of the four develops into a functional megaspore. Examples—*Marsilea*, *Pilularia*.

The secondary sexual dimorphism which distinguishes the megaspores and microspores is of the same general nature as the primary sexual dimorphism which distinguishes the gametes of all heterogamous organisms, but there is, of course, no primary attraction, and there are no swiming organs on the microspores. Since the spores have their sex determined they give rise to distinct unisexual gametophytes. And it is well to call attention again to the fact that the development of maleness and femaleness in the two gametophytes has absolutely nothing to do with any specific or differential heredity which they may possess.

14. Heterosporous pteridophytes with a hereditary constitution which produces a functional gradient that determines a secondary sexual state, either male or female, in the incept of the sorus. Otherwise these plants are essentially the same as type 13. Examples—*Azolla*, *Salvinia*.

15. Some heterosporous pteridophytes in which the sexual states are determined in the incepts of the sporophylls, some passing to the secondary female state and some to the secondary male state. Examples—some species of *Selaginella*.

16. Heterosporous plants which produce a determinate floral axis of the sporophyte of such a nature that the bud passes from the neutral condition first to the secondary male state with the production of stamens (microsporophylls), and then through a sex reversal to the secondary female state with the production of carpels (megasporophylls). This is the usual normal condition in some fossil gymnosperms and in the Anthophyta from Magnolia up to the dandelion. Examples—*Echinodorus*, *Ranunculus*, *Rosa*, *Lilium*, *Oenothera*, *Vernonia*, *Lactuca*.

17. Flowering plants which have a neutral condition of the sporophyte up to the formation of the flower buds. The functional states are so evenly balanced that some of the incepts of the flowers in the same inflorescence fall into the secondary female state and some into the secondary male state and remain in these conditions up to the time of determinate growth. Examples—*Cocos*, *Aesculus*.

18. Flowering plants with a hereditary nature that produces a gradient in the incept of the inflorescence bud of such a nature that a secondary female state is established with con-

sequent production of carpellate flowers for some time and then through a sex reversal ends with the production of staminate flowers. Examples—*Sagittaria latifolia*, *Tripsacum dactyloides*.

19. Flowering plants with the sex conditions just the reverse from that in type 18, the secondary male state developing first and the secondary female state later. Thus the staminate flowers are below and the carpellate flowers above in the inflorescence, coming in the same order as the sporophylls in the typical bisporangiate flower. Examples—*Zizania aquatica*, *Ricinus communis*.

20. Flowering plants and conifers with a hereditary nature that produces functional gradients that secondary sexual states arise long before determination sets in, giving rise to large vegetative branches showing a distinct secondary sexual dimorphism. Examples—*Zea*, *Taxodium*, *Carex lupulina*.

21. Flowering plants and gymnosperms which have a hereditary constitution of such a nature that a functional state arises in the egg, either before fertilization is completed or afterward, which causes one or the other secondary sexual states to be established, the balance falling either to the male condition or the female condition and in consequence the entire diploid sporophyte shows more or less secondary sexual dimorphism. This is the ordinary diecious condition which exists in many degrees of intensity and fixity in various species of the Cycadophyta, Strobilophyta, and Anthophyta. The sexual condition of the individual is often subject to easy sex reversal and re-reversal so that intergrading individuals are produced in special environments. In some species such sex reversal rarely takes place. Examples—*Acer*, *Thalictrum*, *Morus*, *Acnida*, *Cannabis*, *Arisaema triphyllum*.

22. Diecious plants with dimorphic chromosome sets (allosomes) probably always with some differential hereditary potentialities, which may influence the functional gradients on which sex determinations depend. Such plants are subject to sex reversal the same as plants without allosomes. These dimorphic allosome conditions presumably have been brought about by hybridization, as suggested by Miss Blackburn either through the crossing of related species (probably diecious species of type 21) or through a more direct mutation in the species involved which would thus establish a hybrid condition. Sexuality with its reciprocal interaction between male and female gametes made the allosome condition of the sporophyte possible

as a final step in the evolution of the numerous sexual conditions which actually exist at the present time. The allosome condition is the result of sexuality, and unisexuality of the individual is not primarily caused through allosomes, because as stated previously, unisexuality of the higher gametophytes has no correspondence with allosome distribution, and the diecious condition of the sporophyte commonly shows no allosome difference. Examples—*Humulus japonicus*, *Lychnis dioica*.

Anyone who knows anything at all about the evolution of organisms in general and of plants in particular knows that allosomes are not at the basis of sexuality nor of the sex conditions but are mere incidents in the evolutionary development of the various sex conditions. It is also evident that there can be no Mendelian factors for sexuality expressed either as maleness, femaleness or neutrality. When allosomes of a differential nature are once established there may be differential varieties of pollengrains or different varieties of sperms which might react in a distinctive manner to the eggs at the different levels of the gradient through which the egg passes. But in the angiosperms, since there is no free interaction between egg and sperm possible but the egg must unite with whatever type of sperm that the pollentube brings to it or remain unfertilized, it is reasonable to assume that the egg is as evenly balanced as it is in the diecious species without allosomes and which usually produce about an equal number of staminate and carpellate individuals. Then the slight differential condition between the two types of sperms containing the two types of allosomes would cause the functional gradient to go up or down as the case may be and thus put the zygote on the road toward maleness or femaleness. This is probably the correct view of the matter in harmony with the general phenomena of sexuality in both plants and animals. The allosomes are neither sex determiners nor sex producers, nor do they contain sex genes or potentialities but they may and probably do contain differential physiological factors which may be only of a very slight influence after all but are of sufficient force to change the gradient in the evenly balanced fertilizable egg. When the sexual states are once established, differentiation in the male condition or the female condition will amplify the given sexual state, and in some, depending on the general hereditary constitution, the established sexual state will become so extreme that it is practically impossible to throw the system over into the opposite condition,

while in others this is very easily done. Thus we see how the sex of a diecious plant with allosomes can be completely reversed, because the allosome although present in every cell is neither a sex determiner nor a sex producer. This result follows because, as stated above, the allosomes do not possess any factors which are Mendelian sex determiners.

There are, of course, many types of hereditary constitutions, besides the 22 outlined above, which give distinctive functional gradients and functional states with distinctive phenomena of sex determination and sex conditions but the 22 types given show all the phases that one usually has to deal with in a practical way. In all these cases it is, of course, understood that the herditary expression is taking place in a given normal environment. With a change of environment the same hereditities may and often do produce quite different expressions.

CONSIDERATION OF SPECIAL CASES OF SEX DETERMINATION.

THE HEMP (*Cannabis sativa*) probably does not contain allosomes but it is a typical, dimorphic, diecious species. Sex reversal can be brought about in any degree up to complete reversal to the opposite condition. In reversal, this species shows a gradation of conditions from no reversal whatever to complete change to the opposite sex. This series gives absolutely no warrant for assuming a multiple factor series of any kind. The result is due to degrees of differentiation and inequality in detail of environmental conditions. That this is true can be demonstrated through rejuvenating the individuals and then causing reversal in the second differentiation cycle when there was none at the first. Hirata apparently found that selfed carpellate plants tended to repeat the carpellate condition while selfed staminate plants produced both sex conditions more readily. If such a condition really exists it indicates that the pollen and sperms produced on the carpellate plants, although they proceed far enough in catalase reaction and other peculiarities to develop the primary male state in the sperms are, nevertheless, not extreme enough to tip the balance in the egg toward maleness, although some individuals are apparently more strongly female than others. Since the selfed staminate plants tended to produce both carpellate and staminate individuals we can assume that while the sperms are all in the normal, extreme male state, the eggs from these reversed plants

to develop or function at all must manifestly tend slightly toward the female condition at the time of fertilization. Thus when fertilization takes place with self sperms the sex balance works in the normal way as when cross fertilization occurs between a carpellate and a staminate individual. However, it must be recognized that the performance of any individual in any given environment is not to be taken as evidence of its sex potentiality since we know that these selfed reversed plants necessarily had a potentiality to produce both sexes under the conditions in which they were growing. The given expression is then nothing but an indication of the ease or degree of sex reversal in the environment in which fertilization and development are taking place.

The fact of sex reversal and the zonal development of sexual states in monecious plants and the similarly induced zonal development of sexual states in diecious plants like the hemp have robbed the sex-gene hypothesis of any plausibility it might have when considered in ignorance of these primary phenomena. In hemp, the writer took a pure carpellate plant and by a process of rejuvenation caused a zone of pure male expression with the production of typical and normal staminate flowers. Later this same branch reversed again to the pure female expression. Such a procedure cannot only be produced experimentally but may be observed in various diecious species out in the field. Any notion that the changes are due to losses of chromosomes or genes must be characterized as absurd in the extreme. With the advancement of our knowledge of producing rejuvenations and repeated rejuvenations, accompanied by re-reversals of the sex condition, no one will probably have the simplicity to continue to believe that chromosomes play any such hide and seek game of "now you have it and now you haven't."

HUMULUS JAPONICUS. This plant has the allosome formulæ, carpellate AA and staminate AB. The carpellate plants are easily reversed to the staminate condition, to a greater or less degree, in spite of the presence of the AA set of allosomes and the staminate plants are easily reversed to the carpellate condition in spite of the presence of the AB set of allosomes. It is evident that the allosomes are not sex-determiners and probably not even sex-producers.

HONEY BEE (*Aphis melifica*). The honey bee furnishes conclusive evidence that sexuality is primarily not at all dependent

on Mendelian heredity, although we know that if the chromosome hypothesis of Mendelian segregation is correct, then Mendelian heredity is but a result of sexuality. The facts worked out by entomologists on the honey bee are apparently as follows: The workers and queens are females with the diploid complement (2x) of chromosomes. The workers are neuter females, having been developed as partial neuters through the manipulation of their environment by their nurses themselves during the developmental period and because the egg was deposited in a certain type of cell. The drones or males are hapolid (x) individuals having been developed parthenogenetically. There is, therefore, no evidence that an allosome is present or ever was present in the race. It is impossible to obtain such evidence unless the female had an AB set of allosomes in which case the male might have an A or a B. But the only difference seems to be that the female has a double complement of chromosomes and the male a single complement. If a worker develops functional femaleness, as is sometimes the case, all of her eggs develop drones. If a queen bee runs out of sperms, she produces nothing but drones no difference where the eggs are laid. In this case the drones developed in worker cells are said to be somewhat smaller than the normal.

Now the queen is a normal female with the double complement of chromosomes. These chromosomes have a hereditary constitution of such a nature that the diploid condition always throws the functional gradient of the developing egg toward the female condition or rather keeps it from going to the male condition. The eggs are produced through a reduction division in the usual way, all having the same kind of haploid complement of chromosomes. All of these eggs come from cells in the secondary female state and pass on to the development of the primary female state with the plus (+) reaction toward the sperms which are in the primary minus (—) or male state. So the queen may lay large numbers of eggs all fertilized. When she lays an unfertilized egg into a drone cell, this egg was also in the primary female state but because it is not fertilized its gradient goes over through the neutral state and then is reversed to the secondary male state. Most haploid eggs of plants and animals have a hereditary constitution that ends in stagnation and death when they reach the neutral condition, unless a special stimulus is applied from the outside to induce artificial parthenogenesis. But as indicated, the heredity

of the honey bee is such that the passing of the functional gradient through the neutral point does not lead to inactivity but rather to continued activity over to parthenogenesis and the secondary male state. The egg being now in the secondary male state develops a male with the haploid complement of chromosomes in its cells. There is, therefore, no proper reduction division at the maturation of the spermatozoa but the cells pass on from the secondary male state to the primary male state in the mature spermatozoa with the minus (—) sex reaction toward the eggs. Now we see that the same hereditary constitution, the same complement of chromosomes, without any material change whatever has passed from the secondary female state of the incipient egg, which state was handed over directly from the secondary female state of the queen's body, to the primary female state, to the neutral state, to the secondary male state of the drone's body, to the complete primary male state of the spermatozon. Yet there are numerous text-books, in perfectly good repute today, which by the easy method of reasoning in a circle pretend to explain such a simple series of evident phenomena by an appeal to the sex chromosomes and Mendelian sex gene hypothesis!

APHIDIDÆ. The condition in various species of plant lice is equally clear in demonstrating that allosomes follow the sex rather than determine it. In the aphids the summer environment gives rise to parthenogenetic diploid females and these females reproduce themselves for some time by producing diploid parthenogenetic eggs. Later in the season, however, a change takes place and these females produce cells of two kinds, some in the secondary male state and some in the secondary female state. The oocytes in the female state divide as before and thus the resulting eggs are normally diploid again. But the oocytes which have passed over to the partial male state undergo a change. Under the partial male state a synapsis is accomplished between the two pairs of allosomes although the autosomes are not so affected. The allosomes are so held together that two are lost out in consequence, and the resulting egg, although it has the diploid complement of autosomes, has only two allosomes instead of four as are present in the egg developed under the female state. Since the male and female states are developing further during the division states and the completion of maturation, they become large and small eggs when compared with each other. There are therefore large and

small eggs just as there are megaspores and micropores in the heterosporous plants and for the same general reason. The small eggs, being in the secondary male state, develop into male aphids and the large eggs, being in the secondary female state, develop into female aphids, just as the microspores develop into male gametophytes and the megaspores develop into female gametophytes, no difference what their allosomes or special hereditary constitutions may be. The sexual state determines the disposition of the allosomes in these aphids rather than that the allosomes are determining the sexual state.

DOMESTIC CHICKEN. In the chicken, the diploid individual with the female state contains but one allosome while the individual in the male state contains two. The allosome formula is thus female Ao, and male AA. Now in this case there is no difference in the hereditary factor constitution of the two individuals. The only difference is that the male is diploid in respect to the allosome A and the female haploid. The difference of the single or double state of the allosome may again effect the functional state of the egg as explained previously and so during the fertilization process the sex balance falls in the direction as indicated by the normal allosome formula of the sexual individual. But that the allosomes are neither sex determiners nor sex producers *per se* is plainly shown in the fact that a hen may be transformed into a completely functional rooster in spite of the fact that every cell in her body has the haploid condition of allosome A. The rooster may also go a long way in the transformation to the female condition, in spite of the fact that the allosomes in all the cells of his body are diploid.

VALLISNERIA SPIRALIS. Although the matter seems not to be definitely cleared up, according to Winge, it appears as though in Vallisneria the staminate plant has one less chromosome in the diploid generation than the carpellate plant. The formulæ for the sporophytes would then be: Carpellate, AAxx; staminate, Aoxx. This would be just the opposite from the condition in the chicken. There would be no fundamental difference in herditary potentiality between the male and female conditions except that one has the allosome A diploid and the other haploid.

Now it should be possible to find related species which could hybridize with resulting offspring in which the factors for various physiological gradients and conditions would be so evenly balanced that during the ontogenetic development the

sex determination balance would swing several times in one direction or the other giving rise to sex mosaics. In disturbed *Arisaema triphyllum* inflorescences and in the Indian corn tassel as well as in the flowers of hemp and Japanese hop such sex mosiacs are often in evidence. In fact any sex intergrade, is properly considered a sex mosaic, produced by the play of changing physiological gradients. In cases where the sex is reversed after rejuvenation in a second differentiation cycle, the process is fundamentally the same as when the sex mosaic appears in the first or normal cycle.

The more recent attempts at finding out the conditions of sex determination from self-pollinated reversed plants are again subject to misinterpretation long before any complete data are at hand for making categorical statements. In hemp for example, Hirata speaks of "females" and "female intersexes," but these terms can mean nothing except that under the given conditions the sex expression of the individual happened to be of that nature. We know that the presumption is quite firmly established at the present time that any hemp plant has the potentiality to be either "pure" male of female or a male or female intersex by simply bringing it into the proper environment. Labels put on an individual because of a single chance performance can mean nothing from the standpoint of critical analysis. Not all hemps have the same heredity in respect to the gradients established under a given environment. Some varieties produce intermediate individuals in the normal summer environment and some do not. But in both of these two types nearly all the individuals change to the intermediate condition when grown in a proper short light environment. Other conditions being proper, the change in sex expression is proportional to the length of daily illumination. Therefore it means nothing to label an individual as a "female" or a "male" or an "intersex" unless the label refers merely to the temporary mode of expression and not the potentiality through which the expression is produced. The label cannot imply a difference in constitution. Therefore, the conclusions drawn from such genetic phenotypic phenomena are of no primary genetic significance. Now in my experiments on hemp there was always a small percentage of individuals that did not change under the treatment given. But some of these individuals did change with a second treatment. There is no question but that all will change with proper environmental control. Furthermore, the degree

of sex reversal in the hemp plants, if estimated by the percentage of staminate and carpellate flowers produced, will be practically different for every individual. The diecious hemp and the diecious allosome-containing Japanese hop show the same gradation series as is shown in the sex reversal of the tassel by both the ordinary heterozygous Indian corn varieties and by highly imbred Indian corn, which are normally monecious. These sex series are fluctuations and one could manipulate the expression in such a way that there would be a continuous gradation series from zero up to one or two hundred degrees. These fluctuations are the facts which need explanation, and not only the fluctuations among individuals but the fluctuations of the same individual under different, rejuvenated ontogenetic cycles, which, as the writer has shown, can be easily produced. One may ask the questions: Why does the percentage of individuals showing sex reversal correspond with the ecological series? What makes the individual flucutate in sex expression with the environment? Why are the reversal series of the same type in the monecious species as they are in the diecious? The real crux of the matter is that a variety that is expressed as an intersex or hermaphrodite will under another environment be of a single or pure sex expression, and one that is expressed as pure will under another environment be expressed as an intersex or hermaphrodite. The thing works both ways as is evident by comparing the experiments on Indian corn and hemp. Until it is shown that this cannot be done there is nothing to argue about.

As to the fact that plants coming from selfed, reversed carpellate plants tend to produce femaleness and rarely decided male conditions, this should be expected since under the ordinary conditions one would expect the male gametes produced on the carpellate plant to be not extreme enough to cause the zygote to change its determination from the femaleness already present to maleness. And in the same way the staminate plant might in many cases tend to perpetuate maleness. If it does not do so in a given variety, it simply means that the eggs which are produced on the reversed parts of the staminate plant, because of the high metabolic activity of the organism as a whole, are not viable or functional unless they are developed to the extreme female condition, in which case they would then follow the usual method of determination and part fall to the male condition, on being fertilized and part to the female.

We know from experiment that the process of differentiation is not to be counted upon to give the same degrees of conditions in various specific cases. The physiological nature of sex must present a diversity of results in different species and one can only find out what the usual reaction is for a given environment with a specific hereditary complex by actual experiment. The next case may react quite differently. The facts obtained through breeding and ecological experiments can be explained by the fundamental physiological theory. They cannot be explained on the assumption of Mendelian hereditary factors. The vast majority of the facts of sex in plants and animals give a flat contradiction to any Mendelian hypothesis of sex whatever. What is inherited is the potentiality of sexuality, but this cannot be shifted out of any sexual protoplast. The sexual states developed as maleness or femaleness are not inherited as Mendelizing units, but, as explained earlier in this and other papers, in the vast majority of organic sexual types the sex is not changed nor determined by the shifting of the Mendelian factors. The factors are shifted while the sex condition remains unchanged.

At present it is impossible to think of Mendelian heredity except in terms of chromosome-linked heredity. Ever since the writer first discovered the true nature of the reduction division, while studying the cytology of *Lilium philadelphicum* in 1896-7, it has been evident that all normal Mendelian hereditary phenomena correspond with the aggregations and segregations of chromosomes during fertilization and reduction. The reduction phenomena were confirmed by a series of further investigations, one on *Erythronium* before Mendelian heredity was made known, and one on *Lilium tigrinum* several years after the Mendelian view of heredity was established. These laborious investigations established a proper basis for the explanation of Mendelian heredity. They were not accepted at first until the shere weight of Mendelian phenomena compelled a proper consideration. In the mean time a fundamentally false explanation of "crossing-over" has been foisted on an unsuspecting scientific public, which is absolutely without any cytological basis. True crossing over is a primary sexual phenomenon and a reasonable hypothesis of its cause and action can be developed. Instead of this we have the spectacle of a most profound cytological vagary which never did and never

could take place according to all the cytological evidence we now have.

As stated above, my discovery of the qualitative reduction division laid a firm cytological basis for an explanation of Mendelian heredity. In the meantime no other phenomena have been found which can explain Mendelian ratios, and linkage phenomena. Thus, for the present at least, Mendelian heredity rests on a firm chromosome foundation. But on the other hand, the phenomena of sex determination and sexuality show no such general correspondence. In fact, as has been repeatedly emphasized, there are only a few types of organisms where sex phenomena and chromosome phenomena coincide, and the vast majority of the most evident phenomena of sex are flatly contradictory to any Mendelian explanation whatever. The most evident contradiction comes in the 150,000 heterosporous plants in which the segregation of Mendelian heredity with the chromosomes during reduction never results in a segregation of sex. One might as well attempt Mendelian explanations for the transmission of heredity in the nonsexual Protophyta as to attempt to associate the cause of sexual states with chromosome shiftings. Those who speak innocently of Mendelian sex phenomena in the higher plants either do not know the chromosome history of these plants or else do not comprehend the presence of the non-correspondence. Neither secondary sexual states nor the sexual dimorphism of the reduction spores, nor the gametophytes which come from them, nor the primary sexual states of the gametes produced by them is in any way affected or influenced by the segregation of the chromosomes with their possible hereditary potentialities. Organisms either inherit a sex potentiality and are therefore sexual organisms or they have no such potentiality and are then nonsexual organisms. The sexual states which arise in organisms with sexuality and expressed as male, female, or neuter are caused by the interaction of physiological and ecological conditions.

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